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NESTS OF TERRESTRIAL SPIDERS MAINTAIN A PHYSICAL GILL: FLOODING AND THE EVOLUTION OF SILK CONSTRUCTIONS

Jerome S. Rovner

Department of Zoological Sciences
Ohio University, Irvine Hall
Athens, Ohio 45701

ABSTRACT

Individuals of *Dysdera crocata* and *Ariadna bicolor* usually drown during the first day of submersion in aerated water (21 to 25°C). However, if submerged while in their nests, they remain capable of activity for up to 10 days. Those residing underwater for the average of 3 days or for a longer period cannot continue to rely on the original oxygen supply of the nest's air store, which is less than a 2-day supply. A decrease in dissolved oxygen in the water, as measured in closed systems, indicates that the bubble held in the nest acts as a physical gill, with oxygen uptake averaging 3 to 4 $\mu\ell\ h^{-1}$ for the nests of adult spiders. Thus, the spider's survival underwater depends on the nest's preventing the Ege effect from diminishing the bubble. Flooding, which could occur in any of the terrestrial habitats of various ancestral arthropods, should be included among the several factors hypothesized to have favored the evolutionary origin of silk nests in spiders and similar constructions in certain other arthropod taxa.

INTRODUCTION

The use of silk by submerged spiders to maintain a bubble that acts as a physical gill has been shown to be significant only in the aquatic species *Argyroneta aquatica* (Clerck) (Schollmeyer 1913, Braun 1931, Thorpe 1950). While the ability of coastal species to survive tidal sumergence attracted the attention of many workers (e.g., Abrahams 1924, 1926, Arndt 1915, Bethge 1973, Bristowe 1923, 1930, 1931, Heydemann 1967, Lamoral 1968, McQueen and McLay 1983, McQueen et al. 1983, Schaefer 1974, 1976), only McQueen and McLay included tests of spiders that were inside silk nests. They found that the physical gill effect did not substantially increase the survival time underwater in the intertidal spider *Desis marina* (Hector), since this spider's nest, built beneath the holdfasts of bull kelp, was always within a cavity that held an air supply adequate for many days of submergence. But what of inland, terrestrial, ground-dwelling spiders trapped in their nests during rain-caused flooding, wherein the nest surface itself is directly covered by water for days in many cases?

Many spiders carry a bubble when submerged, which was shown to act as a physical gill in two intertidal species (Lamoral 1968), just as it does in many insects (Ege 1915, Thorpe 1950). In all spiders examined so far—even *Argyroneta aquatica*—the hydrofuge hairs are not specialized like the critically spaced

hydrofuge hairs of certain aquatic insects; therefore, spiders cannot maintain a bubble or air film as a permanent plastron (Thorpe 1950). The bubble gradually disappears during a number of hours because of the outward diffusion of nitrogen (the "Ege effect"). Without a bubble, the spider cannot extract oxygen from the water, and it drowns.

Like the wintertime web of *A. aquatica*, the silk nests of various terrestrial spiders might prevent the dissolution of the entrapped bubble, thereby maintaining a physical gill during prolonged submergence. I decided to investigate this possibility, being curious about how our local, ground-dwelling spiders survive rain-caused flooding.

Since many or most terrestrial spiders climb vegetation to escape rising flood waters (Cooke 1962), I chose to study two species which spend much or all of their time in silken structures built among or beneath stones. *Dysdera crocata* C. L. Koch (Dysderidae) builds closed sacs used for molting, brood care, and retreats that may be occupied for over a month (Cooke 1965) and also can be found beneath lumps of mud in marshes (Cooke 1967). *Ariadna bicolor* (Hentz) (Segestriidae) dwells in a tubular retreat from which it darts for prey capture. (To save space, I shall use the term "nest" henceforth for both types of structures.) I assumed that these spiders tend to remain in their nests at the onset of flooding in nature, since they always did so in laboratory simulations. Such behavior was observed in the field in a terrestrial clubionid (*Clubiona phragmitis* C. L. Koch) by Bristowe (1931), who found the spiders "enclosed in dense silken cells attached to the underside of stones the tops of which were only just appearing above the surface of the lake, which had overflowed its ordinary boundaries."

In the present laboratory study the spiders survived as long as 10 days in their nests under water that was relatively warm, while they typically drowned within 12-24 h if outside the nest in such water. Measurements made with oxygen electrodes showed that oxygen diffuses from the water into the nests, thereby supporting an hypothesis that the nest-maintained bubble serves as a physical gill, a heretofore unsuspected adaptive advantage of the nests of terrestrial spiders. A possible flood-survival role for the silk added to the burrows of ancestral spiders was suggested by this study.

MATERIALS AND METHODS

I collected the two species of spiders beneath or between loose bricks and stones in locations shaded by vegetation (summer and fall, 1983 and 1984; Athens County, Ohio, USA). Vertically standing plastic vials (24 mm diameter, 50 mm height for small individuals; 32 mm diameter, 70 mm height for large) housed most spiders. Nests were built where the vial wall and bottom came together, often beneath a piece of plastic screen that leaned against the wall. Drinking water was injected through the air hole of the cap every few days. Some *D. crocata* were housed in plastic cages (7.0 × 12.5 × 7.0 cm high). *D. crocata* preyed on isopods, while *A. bicolor* fed on *Drosophila melanogaster* and *Tenebrio molitor*. Room temperatures ranged from 21 to 25°C, depending on the time of year. All the housing containers were placed behind and beneath cardboard sheets to maintain low illumination, like that found beneath stones. I used a Kahn electronic analytical balance (model TA-450) to weigh spiders. Means are followed by standard errors of the mean.

Survival Times After Submersion.—To compare resistance to drowning in spiders without vs. within their nests, I submerged them 10 cm below the surface in aerated aquarium water. Spiders without nests were given a strip of paper for a foothold. I used a syringe to withdraw the bubble trapped beneath the screen cover of the vial after submergence. The vials were held horizontally beneath glass bowls and had their screen-covered openings facing the center of the 5-gallon aquarium, where bubbles issued from an air stone connected to an air pump, a setup modified from Lamoral (1968). Cardboard sheets over and around the aquarium insured dim illumination, except at brief intervals when I removed them to view the spiders. Spiders in nests were made partly visible by backlighting with microscope illuminators during the brief inspection. Water and home-vial air temperatures were similar, which minimized acclimation effects.

Spiders without nests were removed from the water after a limited period, usually 12, 18, 24, or 36 h; placed ventral side up (if unable to stand upright); and given 1 day to recover. Spiders within nests were checked at intervals; I tapped the vial and, if there was no response, prodded the nest with a dissecting needle inserted through the screen cover of the vial. If still no response, the vial was removed from the water and the nest was opened. Such spiders soon showed activity and, therefore, could have remained submerged a longer time. These individuals constituted the category of spiders that had "limited residency."

The majority of nest submersions involved "unlimited residency," in which case the spider was removed from the aquarium only after it had "chosen" to leave its nest. Since spiders without nests can survive some number of hours underwater, the time recorded for the duration of each unlimited residency represents the time spent in the nest plus some unknown amount of time in the water outside the nest, the latter not exceeding the nighttime interval (maximum = 8 h).

I estimated nest volume in *D. crocata* by filling empty nests with water from a 0.01 ml-calibrated syringe; values were rounded up to the nearest 0.05 ml. Since the spider would occupy some space (roughly 15%), nest volumes exceeded maximum possible bubble volumes.

Oxygen Diffusion into Submerged Nests.—To test an hypothesis that the nest-trapped bubble serves as a physical gill, I used closed systems based on two setups, A and B, each providing a check for the other. I compared the decrease during 2 h in the percent oxygen saturation of previously well-aerated aquarium water surrounding an inhabited nest to that of such water (fresh sample) surrounding the same nest, now empty and flattened. A similar approach, employing a micro-Winkler technique, established a physical gill function for the bubble adhering to the body in two species of intertidal spiders (Lamoral 1968).

In setup A, a housing jar served as the test chamber and a Markson oxygen meter (model 230) for the measurements. I added a piece of plastic screen shaped to encourage nest construction by the spider dwelling near the bottom of each jar (jar size: 25 mm diameter × 58 mm high).

To make each measurement I used the following procedure. After turning the jar to a horizontal position, I placed a tiny (2.0 × 8.5 mm) stirring bar inside near the opening and taped a magnet to the jar's exterior at the bar's location, the latter insuring control of the bar's location during subsequent steps. Returning the jar to a vertical position, I slowly filled it with aerated aquarium water. Next, the jar was screwed upward into a cap through which projected the

vertically clamped oxygen probe. (Aquarium sealer filled the tiny gap between the cut surface of the cap and the probe.) I then placed the probe and its now-attached jar in a horizontal position and removed the magnet. (If a bubble were trapped, appropriate steps were repeated to eliminate such a source of error.) Finally, the probe/jar were positioned 5 mm above the center of a magnetic stirrer, so that the bar would spin at the far end of the jar, away from the spider's nest (Fig. 1).

For the initial and each of the two subsequent hourly oxygen readings, I switched on the stirrer and oxygen meter, allowing 1.5 min for equilibration before taking the reading; the stirrer and meter were then switched off. Readings were made at 22 to 24°C, depending primarily on room temperature but also, as to the initial reading, on my handling of the jar during the closure procedure. Because of the latter, the oxygen value for the initial reading was later calculated to the higher value it would have at the 1 to 2° lower temperature recorded at the two subsequent hourly readings. (A thermistor inside the probe of the Markson meter provided all the temperature readings in setup A.) The volume of water present in the closed jar with the probe tip inserted was 19 mℓ.

Setup B involved a YSI oxygen monitor (model 53), a macro-bath stirrer assembly (YSI 5302), and a circulator (Forma 2066). The advantage of this setup was in having a constant water temperature (±0.02°) throughout each run and among all runs. I used 25°, the lowest temperature of the range recommended for the YSI oxygen monitor, to stay close to the temperatures used in setup A, as well as to avoid subjecting the spiders to a significant change in temperature from that in their home cage; previous thermal history affects the metabolic rate measured at a sufficiently different temperature (Anderson 1970). In setup B the volume of water was approximately 25 mℓ and, unlike setup A, the stirring bar spun and the oxygen electrode was on throughout the 2-h period. Individuals ranged in mass from 70 to 158 mg (mean = 116 ± 36).

The disadvantage of setup B was that the bath-stirrer required that the stirring bar be placed on the bottom of the chamber beneath a screen. This prevented use of the measurement chamber as a site for nest building. Instead, laboratory nests were built inside 10 mm-diameter × 25 mm plastic screen (no. 18 mesh) cylinders offered to some of the spiders in their home cages (Fig. 2). A few nests collected intact in the field were placed into stainless-steel screen (no. 30 mesh) holders; two such nests were subsequently revealed to be shared with broods—a 121-mg female with 80 young (88 mg) and a 158-mg female with 115 young (155 mg) (Fig. 3).

The method of calculating oxygen consumption was as follows. Oxygen concentration (mg/ℓ) at each temperature was obtained from an appropriate table of oxygen solubilities in water (Wetzel 1983). (Since such tables are for pure rather than aquarium water, values determined in the present study are only approximate.) Multiplication by 0.70046 converted the value for mass to a volumetric value (mℓ/ℓ (ibid.), which provided the basis for values expressed as μℓ/mℓ. Multiplication of the latter by the total volume of water in the chamber (19 or 25 mℓ) gave an approximate value for the total volume of oxygen present in such a volume of water under ideal aerated conditions. This figure was then multiplied by the difference in percent oxygen saturation between the initial and final readings, thus yielding a rough estimate of oxygen decrease in the water

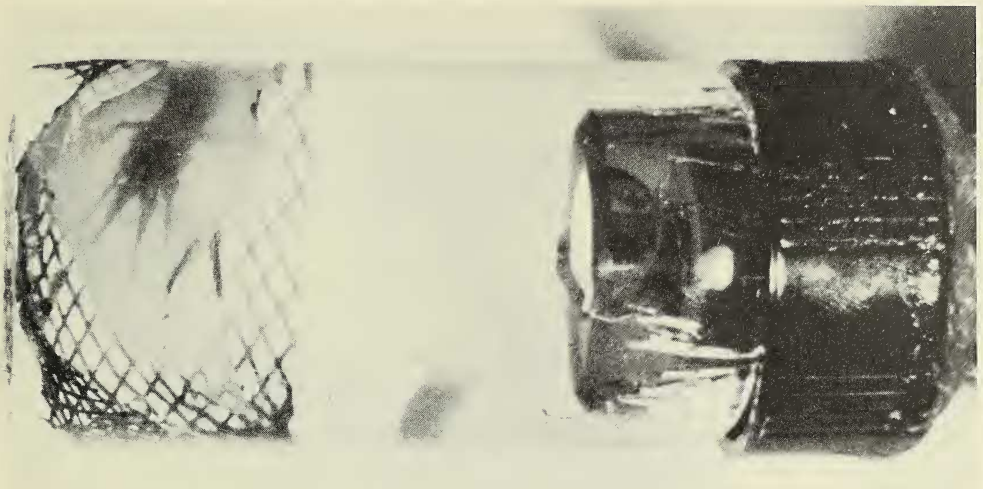

Fig. 1—Setup A for determining oxygen diffusion into submerged nests of *Dysdera crocata*. The spider is visible within the backlighted nest, which was built upon plastic mesh at the bottom of the originally vertical jar (jar diameter = 25 mm). The stirring bar is located to the left of the probe, which projects through the cap (at right). This photograph was not taken during an actual run.

during the 2-h period. Half of this value then expressed the approximate drop in oxygen concentration per hour ($\mu\ell\ h^{-1}$).

Since a determination of actual oxygen consumption was not a goal of my study, I did not control for possible minor effects of diel variation. Starving the spiders prior to testing did minimize the effect of food assimilation (Anderson 1970).

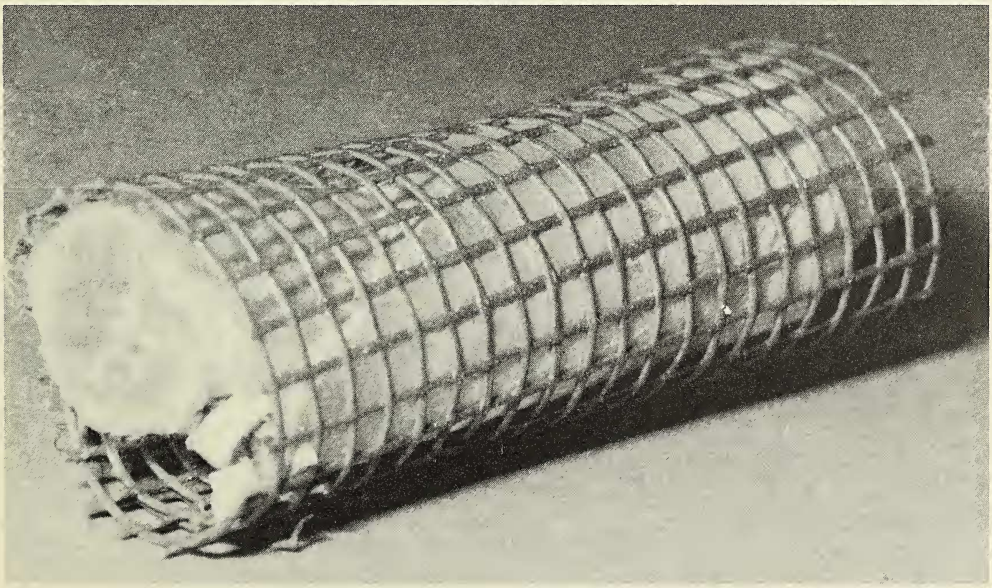

Fig. 2.—Plastic screen cylinder (length = 25 mm) containing a silken nest built by an adult female *Dysdera crocata*.

Fig. 3.—Field-collected, debris-covered brood nest of *Dysdera crocata* just removed from the water after a 2-h run in setup B. The interior and inhabitants remained dry during submergence in the swirling water. (Body length of now-emerged female = 13 mm)

RESULTS

Survival Times After Submersion.—Spiders submerged without nests ($N = 49$) crawled around the vial at intervals, *D. crocata* moreso than *A. bicolor*. *D. crocata* lost its adhering bubble and drowned sooner than did *A. bicolor*. When removed from the water after 12 h submergence, 10 of 14 *D. crocata* had drowned; all 10 of those submerged for 18 h drowned (mean for drownings = 15.0 h). (Tests of 60 spiderlings of *D. crocata* showed them to be no more resistant to drowning than the much larger instars: 9 of 20 drowned in a 6-h test; 19 of 20 in a 12-h test; and all of 20 in a 24 h test, all tests at 24°C.) Since *A. bicolor* often survived 12 h in preliminary trials, it was tested for longer periods: 8 of 11 drowned within 18 h; 7 of 9 within 24 h; and all of 5 within 36 h (mean for drownings = 24.2 h) (Fig. 4).

Spiders submerged while in their nests ($N = 35$), although inactive for most of the time, occasionally groomed, deposited silk, and re-positioned themselves; some molted. (I did not determine whether spiders in nests that had not been submerged showed similar levels and types of activity. I was interested only in whether spiders in submerged nests entered a state of immobility suggestive of very low metabolic rates, precluding "normal" behavior; they did not.) Seven spiders that had not responded to direct prodding of their nests emerged from their subsequently opened nests; i.e., they had not drowned during the period of "limited residency." During one inspection an *A. bicolor* left its nest (after 5 days of submergence), wandered in the water for several minutes, and then returned to its nest for an additional day of residency.

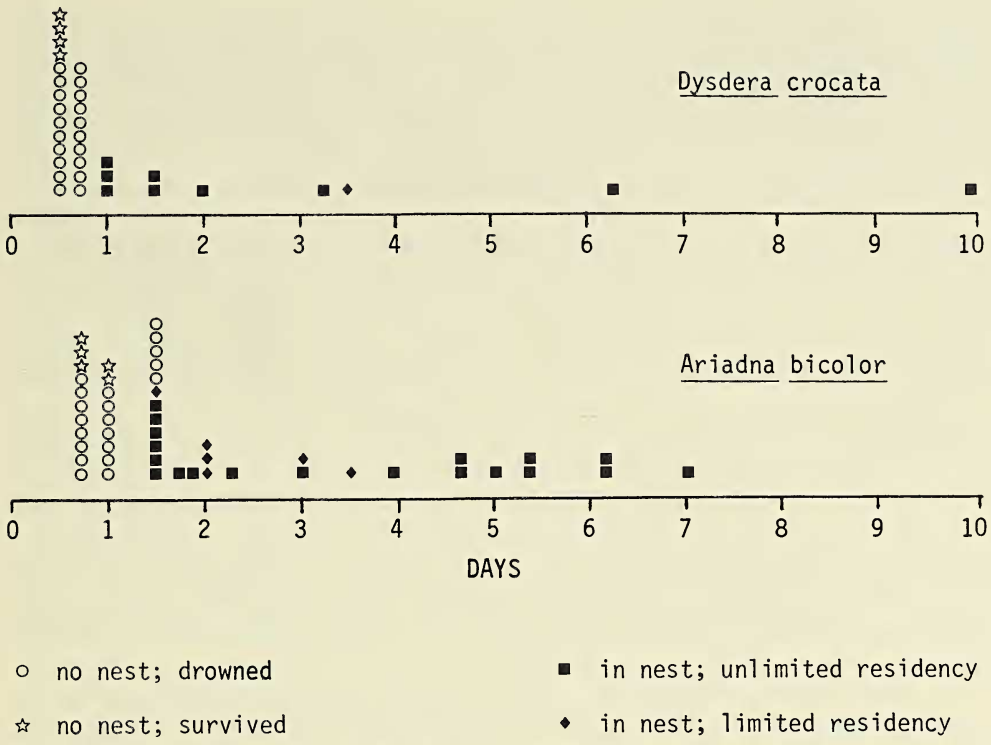

Fig. 4.—Duration of underwater survival in two species of terrestrial spiders tested within (N = 35) or without (N = 49) their nests.

Throughout nest residency, spiders were inside a typically ovoid bubble that had stabilized at a length greater than that of the spider's body, although initial reduction in size had occurred following submergence. For example, after 6 days a *D. crocata* still had a bubble large enough to allow the spider to make a 180° turn and to stand with its legs spread as if on an open surface. However, in some very thin-walled nests, the bubble decreased to a size little wider than the spider's tightly drawn-in legs; indeed, a few individuals rested with their anterior legs projecting through a nest opening into the water. The nest volumes in *D. crocata* ranged from 0.15 to 0.60 ml for solitary individuals and from 0.75 to 0.80 ml for nests shared by females and their broods.

Most spiders eventually left the nest, even though the bubble was still present inside. They took part of this nest bubble with them when leaving, carrying the adhering bubble primarily on the opisthosoma and sometimes being buoyed up in the water to a variable extent as a result.

For spiders residing at least 1 day, the duration of nest residency in *D. crocata* was 3.1 ± 0.9 days (N = 10); maximum = 10 days (21°; 43 mg spider). For those *A. bicolor* residing at least 1.5 days, nest residency = 3.2 ± 0.4 days (N = 25); maximum = 7 days (23°; 20 mg spider) (Fig. 4). Although not included in the above data, even females with spiderlings or eggs eventually left the nest; however, they remained near the nest with the aid of a dragline.

Oxygen Diffusion into Submerged Nests.—Decreases in relative oxygen saturation readings were greater for water surrounding inhabited nests than for water surrounding empty nests (Table 1). Decreases in readings were due partly

Table 1.—Mean (± S.E.M.) decrease during 2 h in the relative reading for percent oxygen saturation of water surrounding nests with bubble-enclosed spiders vs. water surrounding empty nests. Setup A had 19 ml of water; B had 25 ml. Significance of differences (one-tailed paired *t*-tests, d.f. = $N - 1$) and mean volume of oxygen entering an inhabited nest are given. Abbreviations: *n*, number of spiders; *N*, number of paired runs; *d*, mean difference; D. c., *Dysdera crocata*; A. b., *Ariadna bicolor*. Two females (*) shared their nests with broods.

Setup	Species	*n*	*N*	Inhabited nest	Empty nest	*d*	*t*	*P*	0_2 entry ($\mu\ell$ hr^{-1})
A	D. c.	3	7	10.1± 1.5	4.6 ± 0.6	5.5	3.51	<0.01	3.1
	A. b.	1	2	6.0± 1.0	1.0± 1.0	5.0	2.50	NS	3.0
B	D. c.	5	5	30.8± 4.6	25.2± 4.1	5.6	4.63	<0.005	4.1
	D. c.*	2	2	62.5±18.6	36.5±20.6	26.0	13.00	<0.025	18.8

to downward drift (which preliminary tests showed to occur at a higher rate in the equipment of setup B than in that of setup A); also I did not assess the measurement errors and the mechanical and electrical drift associated with the use of these electronic oxygen probes. I therefore regarded all readings as relative measures of pO_2. Furthermore, I assumed (but had no evidence) that the rate of drift affected experimental and control readings within each setup similarly, and that the difference between experimental and control readings was an absolute measure of oxygen diffusion into the nests.

The approximate volume of oxygen that entered the nest of each solitary *D. crocata* averaged 3 to 4 $\mu\ell$ h^{-1} (22 to 25°) (Table 1). The diffusion rates for nests with solitary spiders were similar between setups A and B, suggesting that both systems of measurement were reliable. On the basis of mass, group B of solitary *D. crocata* (106 ± 16 mg) showed oxygen diffusing into nests at a mean rate of 0.038 $\mu\ell$ mg^{-1} h^{-1} (25°). (Lacking the mass of one *D. crocata* of group A, I could not make such an estimate from the data of that group.)

DISCUSSION

Spiders submerged while in their intact nests were able to survive for much longer than those outside of nests: *D. crocata* inside nests endured submergence up to at least 16 times (mean = 5.0 times) longer, and *A. bicolor* did so up to at least 7 times (mean = 3.2 times) longer than did conspecifics submerged without nests. Furthermore, the 10- and 7-day maxima for the two species may not be the upper limits for their survival underwater, since they reflected the spiders' "decision" to leave the nest-trapped bubble. Nonetheless, the persistence of the bubble for these many days, unlike its disappearance from the body of "naked" spiders within a matter of hours, indicates clearly that the silken construction can maintain a physical gill far more effectively than can the spider's setae. Also, the ability of the spiders to perform various behaviors, as well as molt, while within the underwater nest shows that the physical gill was able to provide for an adequate level of oxygen diffusion from the aerated water.

The volume of oxygen entering the nest of each solitary *D. crocata*, as estimated from measured changes in percent oxygen saturation of the surrounding water in closed systems, was 3 to 4 $\mu\ell$ h^{-1}. This falls within the range of about 1 to 5 $\mu\ell$ h^{-1} determined as the oxygen consumption rates for 10- to 100-mg individuals of the intertidal spider *Desis marina* in air and at a cooler

temperature (17.5°C) (McQueen et al. 1983). The uptake into the nest on the basis of mass (0.038 $\mu\ell$ mg^{-1} h^{-1} at 25°C) in *D. crocata* was about 30 percent lower than the 0.055 $\mu\ell$ $mg^{-1}h^{-1}$ oxygen consumption rate for *D. marina* of similar mass (100 mg; 17.5°C) in air, which was a rate lower than that of any previously tested terrestrial spider (ibid.).

The very low rate for oxygen diffusion into nests of *D. crocata* may reflect one or more of several factors: (1) *D. crocata* is more "primitive" than *D. marina*, based on the dysderid's possession of paired, anteriorly located tracheal spiracles and the desid's having a single, posterior spiracle. Anderson (1970) found that spiders with relatively primitive respiratory systems generally have lower metabolic rates than do spiders with more advanced respiratory systems. (2) Spiders residing in nests underwater may be less active or have lower metabolic rates than spiders exposed in air-filled glassware, the latter being the arrangement used in oxygen consumption studies. (3) The presence of some material in the nest wall or at the air-water interface may slow gas diffusion. McQueen et al. (1983) suggested that spiders may produce an excretory product or other material that could have caused a reduced rate of diffusion across the bubble-water interface in their study of *Desis marina*. Nonetheless, while the rate of diffusion estimated here for the nests of *D. crocata* may be lower than the rate of oxygen consumption by this species in air, it is clear that the nest-trapped bubble provides a physical gill, just as does the temporary bubble carried on the body of the marine intertidal spiders studied by Lamoral (1968).

Conservative use of the data on oxygen uptake into nests, together with liberal estimates of the amount of oxygen available in the nest's initial air store, indicate that the air store is not adequate for prolonged submersion in *D. crocata*. For example, a 100-mg individual using only 3 $\mu\ell$ h^{-1} of oxygen needs 72 $\mu\ell$ day^{-1}; however, even the largest nest of a solitary *D. crocata* holds <0.60 ml of air, i.e., <120 $\mu\ell$ of oxygen, which is less than a 2-day supply. Likewise, the *D. crocata* that survived 10 days underwater was in a 0.20 ml nest, i.e., <40 $\mu\ell$ of oxygen. Even if it could have survived by consuming oxygen at a reduced rate of as little as 1 $\mu\ell$ h^{-1} (and had the ability to take up oxygen at eventually very low partial pressures), it had less than a 2-day supply in the air store. Thus, the nest's maintenance of a physical gill is probably essential for much or most of the submergence period of spiders residing in nests as long as, or longer than, the average of 3 days.

"The hazard of flooding is a very real one for mygalomorph spiders, whether they live in rainforest or deserts" (Cloudsley-Thompson 1983), just as it is for burrowing lycosid spiders living in salt lakes (McKay 1976), and for numerous other ground-dwelling forms. My findings suggest that the silk nest enables such terrestrial spiders to endure a temporary aquatic existence imposed occasionally during their lives. This is particularly important for any spider trapped while molting (a lengthy process of many hours in primitive spiders) as well as for females and their eggs or offspring, which in primitive forms typically share a nest prior to dispersal of the spiderlings.

Secretion of a silk precursor probably arose in ancestral spiders for the protection of eggs or sperm (J. Shultz, in prep.). Since the earliest spiders were most likely burrow dwellers (Decae 1984), the first non-reproductive use of silk was probably to line the burrow. Due to the surface tension of water, a relatively simple meshwork would have been sufficient to keep excess soil water from

entering a burrow. If the meshwork were later extended to cover the burrow opening, a bubble would have been trapped during flooding, which could occur in any of the habitats of ancestral spiders.

Protection from drowning may have been important for the ancestors of other silk-producing arthropods. Pseudoscorpions use anteriorly secreted silk to build nests for molting, brood care, and overwintering, as well as nests for intertidal sites (Gabbutt 1966, Weygoldt 1969). As to silk-using insects, Hinton (1953) stated that the cocoons of Lepidoptera and Hymenoptera pupating on the ground maintain a physical gill during rain-caused flooding. The same may be true for the silken tunnels of the Embioptera (webspinners). Thus, survival during flooding may have been one of the selection pressures underlying the evolutionary origin or diversification of silk use within each of several arthropod taxa in which shelter construction is the primary use for this secretion. In these groups, as well as in spiders, early adaptations for the improved production and application of silk probably were favored by the multiple advantages derived from building some type of enclosure—protection from predation, prevention of desiccation during drought, and maintenance of a physical gill during flooding.

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